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Interspecific Variation in SO_2 Flux[1]

LEAF SURFACE *VERSUS* INTERNAL FLUX, AND COMPONENTS OF LEAF CONDUCTANCE

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ABSTRACT

The objective of this study was to clarify the relationships among stomatal, residual, and epidermal conductances in determining the flux of SO_2 air pollution to leaves. Variations in leaf SO_2 and H_2O vapor fluxes were determined using four plant species: *Pisum sativum* L. (garden pea), *Lycopersicon esculentum* Mill. *flacca* (mutant of tomato), *Geranium carolinianum* L. (wild geranium), and *Diplacus aurantiacus* (Curtis) Jeps. (a native California shrub). Fluxes were measured using the mass-balance approach during exposure to 4.56 micromoles per cubic meter (0.11 microliters per liter) SO_2 for 2 hours in a controlled environmental chamber. Flux through adaxial and abaxial leaf surfaces with closed stomata ranged from 1.9 to 9.4 nanomoles per square meter per second for SO_2, and 0.3 to 1.3 millimoles per square meter per second for H_2O vapor. Flux of SO_2 into leaves through stomata ranged from ~0 to 8.5 (dark) and 3.8 to 16.0 (light) millimoles per square meter per second. Flux of H_2O vapor from leaves through stomata ranged from ~0 to 0.6 (dark) to 0.4 to 0.9 (light) millimole per square meter per second. *Lycopersicon* had internal flux rates for both SO_2 and H_2O vapor over twice as high as for the other species. Stomatal conductance based on H_2O vapor flux averaged from 0.07 to 0.13 mole per square meter per second among the four species. Internal conductance of SO_2 as calculated from SO_2 flux was from 0.04 mole per square meter per second lower to 0.06 mole per square meter per second higher than stomatal conductance. For *Pisum*, *Geranium*, and *Diplacus* stomatal conductance was the same or slightly higher than internal conductance, indicating that, in general, SO_2 flux could be predicted from stomatal conductance for H_2O vapor. However, for the *Lycopersicon* mutant, internal leaf conductance was much higher than stomatal conductance, indicating that factors inside leaves can play a significant role in determining SO_2 flux.

Plant responses to SO_2 are determined by flux of the pollutant into leaves and by the metabolic perturbations caused by SO_2 and its derivatives inside cells (20, 25). Total flux of SO_2 to leaves has been estimated at between 4 and 180 nmol m^{-2} s^{-1} depending on the SO_2 concentration, plant species, and gas exchange measuring system (25, 26). From 50 to 90% of the SO_2 is absorbed into the plant, while the rest is adsorbed on leaf surfaces, based on both nonradioactive SO_2 and $^{35}SO_2$ uptake measurements (4–7, 9, 10). Variability in plant responses within and between species exposed to the same pollutant concentration have been ascribed to differences in cellular metabolism of SO_2 (13, 16, 18). Without consideration of the actual SO_2 uptake by the plants these conclusions may be erroneous; as differences in SO_2 absorption or leaf conductance of the pollutant from the surrounding air into cells may result in quite different cellular concentrations of SO_2 metabolites within and between species (2–6, 24, 25).

Leaf conductance for SO_2 can be partitioned into parallel and sequential components which can act independently or in concert to control SO_2 flux into leaves (1, 25). Stomatal conductance (g_s) has been described as the sole factor determining SO_2 flux into leaf mesophyll tissues (15, 27, 28). Other researchers found that SO_2 flux is controlled additionally by factors inside the leaves which act in concert with, and in addition to, g_s (12, 16, 25). These divergent conclusions vis-a-vis the role of leaf conductance components in determining SO_2 flux can, in part, be attributed to procedures used in evaluating gas exchange. Researchers have used different methods to determine the relative rates of surface *versus* internal SO_2 fluxes to plants, chamber uptake of SO_2, and H_2S emission from plants during SO_2 exposures (4, 12, 25–27).

The objective of this study was to clarify the relationship between stomatal conductance and internal factors in determining the flux of SO_2 into leaves. The investigation was designed to evaluate the physiological factors underlying this relationship using four plant species previously reported to exhibit differences in SO_2 gas exchange (20, 24, 25, 27). The earlier studies had been conducted under different conditions, but in this study the species were grown and exposed under the same environmental conditions. A further objective of this study was to critically evaluate the procedures for determining, and assumptions used in calculating, surface *versus* internal SO_2 flux and H_2O vapor transpiration, and stomatal, residual, and epidermal components of leaf conductance.

MATERIALS AND METHODS

The four species tested were: *Pisum sativum* L. cv Alsweet (garden pea), *Lycopersicon esculentum* Mill. var *flacca* (a tomato mutant), *Geranium carolinianum* L. (wild geranium), and *Diplacus aurantiacus* (Curtis) Jeps. (a native California shrub). *Geranium* and *Diplacus* have been used in earlier SO_2 flux studies (24, 25, 27, 28). *Pisum* and *Lycopersicon* were used to investigate the effects of SO_2 on stomatal conductance and SO_2 metabolism (19, 21). The *Lycopersicon* mutant has stomata which are permanently open in light and dark, even with environmental stress because of a deficiency in ABA metabolism (14). Thus, *Lycopersicon* is especially useful for studying pollutant flux without confounding stomatal responses, *i.e.* opening or closure induced by SO_2 itself.

[1] Contribution from the United States Environmental Protection Agency's Environmental Research Laboratory in Corvallis, Oregon; D. M. O. was sponsored by a National Research Council Postdoctoral Research Associate Grant.

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Plants were grown in an artificial medium (Promix BX)[2] and watered with North Carolina State University nutrient solution as described earlier (20). *Pisum*, *Lycopersicon*, and *Geranium* were grown from seed while *Diplacus* was grown from softwood cuttings. Plants for gas exchange measurements were cultured in charcoal-filtered air in controlled environmental chambers with light/dark air temperatures of 21 ± 0.5 C/20 ± 1°C, PPFD[3] of 301 ± 18 μmol m^{-2} s^{-1} for the 16 h photoperiod, and light/dark RH of 76 ± 14%/90 ± 14%. *Geranium* and *Diplacus* were grown in greenhouses with charcoal-filtered air until transfer to growth chambers, 7 d before pollutant exposures. The preliminary greenhouse growth was required for *Geranium* and *Diplacus* because these species grew more slowly than *Pisum* and *Lycopersicon*, and thus required extra time before exposure.

To obtain estimates of SO_2 flux to leaf surfaces, plants were sprayed until runoff with 0.1 mM ABA to prevent stomatal opening. This procedure was under the assumption that ABA would induce stomatal closure without affecting flux to leaf surfaces, even though there was no suitable control to test whether the ABA itself was affecting leaf surfaces. An air brush (Badger 250) with nitrogen propellant was used. The ABA was dissolved in distilled H_2O with 1 or 2 drops of Triton X-100 added per 50 ml. Plants were sprayed in the dark just prior to placement in the gas exchange chamber and 2 h before exposure to 4.56 μmol m^{-3} (0.11 μl/l) SO_2.

SO_2 and H_2O vapor gas exchange were measured when *Pisum* had 6 fully expanded leaves, at 19 to 21 d after seeding. *Lycopersicon* had 6 to 8 leaves greater than 20 mm in length, at 26 to 30 d after seeding. *Geranium* had 16 to 33 leaves in a rosette, at 35 to 40 d after seeding. *Diplacus* plants were initially exposed with 7 to 11 pairs of leaves, 24 to 26 weeks after rooted cuttings were planted. Successive measurements were made on several of the same *Diplacus* plants by removing all leaves following one exposure and waiting 25 to 50 d before reexposure until new pairs of leaves had emerged.

Fluxes of SO_2 and H_2O were measured using a whole-plant gas exchange system (20, 23). Environmental conditions were controlled within the chamber around the plant at 305 ± 21 μmol m^{-2} s^{-1} PPFD, 20.6 ± 0.5°C leaf temperature, 21.1 ± 0.4°C air temperature, and 15.5 ± 1.1°C dew point temperature to provide 70% RH, and 15.7 ± 1.1 mmol m^{-3} (372 ± 26 μl/l) CO_2, using procedures described earlier (20). Dew point was maintained by manipulating the amount of H_2O vapor in the incoming air stream by passing the air through a bubbler system. Dew point was measured at the chamber inlet and in the chamber using hygrometers (ElectroMech CTE 84 DR) calibrated at 0°C over ice. SO_2, from a permeation tube housed in a constant-temperature oven, was metered into the incoming air stream and monitored with flame photometric total sulfur analyzers (Meloy models 160 and 185) equipped with H_2S scrubbers. Two SO_2 analyzers were used, one for the chamber inlet and one for air from the inside of the chamber. There was no evidence of any H_2S emissions from any of the four species at the 4.56 μmol[3] m^{-3} concentration of SO_2 used in these studies based on measurements with the sulfur analyzer but without the H_2S scrubbers. Prior to use, the SO_2 analyzers were calibrated with a calibration system (Bendix model 8[illegible]1 DATM Field Calibration System with NBS traceable SO_2 tank).

Losses of SO_2 and H_2O vapor to the empty chamber were determined under the same light, temperature, and dew point conditions as when a plant was present (20). Chamber loss for SO_2 decreased logarithmically from approximately 0.23 to 0.07 μmol s^{-1} over the 8 h exposure period (Fig. 1A). Loss of H_2O remained constant in the chamber after equilibration was reached approximately 1 to 2 h after initiation of the experiment (Fig. 1B). The loss of SO_2 and H_2O vapor was assumed to have been via adsorbtion to chamber walls, tubing, and other components of the exposure system.

The fluxes of SO_2 and H_2O and the components of SO_2 and H_2O conductance for leaves were derived using analog models (1, 23, 25). The fluxes were approximately constant during the hour prior to measurement. Formulae used to derive SO_2 and H_2O flux and conductance are shown in Table I. Projected leaf area per plant (single surface), was measured with leaf area meters (Hayashi-Denko model AAM5 and Lambda Instruments model 3100). The projected leaf area was doubled to account for both leaf surfaces for use in total and surface flux determinations.

The both-leaf-surfaces basis was used for flux calculations. It was assumed to be appropriate as both adaxial and abaxial leaf surfaces were exposed to SO_2 in the whole-plant gas exchange chamber used for these studies. However, to compare the role of leaf conductance components in SO_2 uptake for the four species, a careful consideration was made of the actual relative surface area covered by stomata and, thus, capable of taking up SO_2. Conceptually, this required consideration of the fact that the SO_2 molecules could be absorbed through only one conducting surface (stomata only on abaxial surface), both surfaces equally (stomata equally distributed on adaxial and abaxial surfaces), or stomata unequally distributed on both surfaces.

To determine relative conducting surfaces, stomatal densities on adaxial and abaxial leaf surfaces were determined for the four species. Measurements were made using plants grown only under greenhouse conditions described earlier (20). Measurements were taken from the fourth true leaf above the cotyledons for *Pisum* and from middle-aged leaves for the other three species. The

[2] Mention of trade names or commercial products does not constitute endorsement or recommendation for use.

[3] Abbreviations: PPFD, photosynthetic photon flux density. Additional abbreviations and formulae are found in Table I.

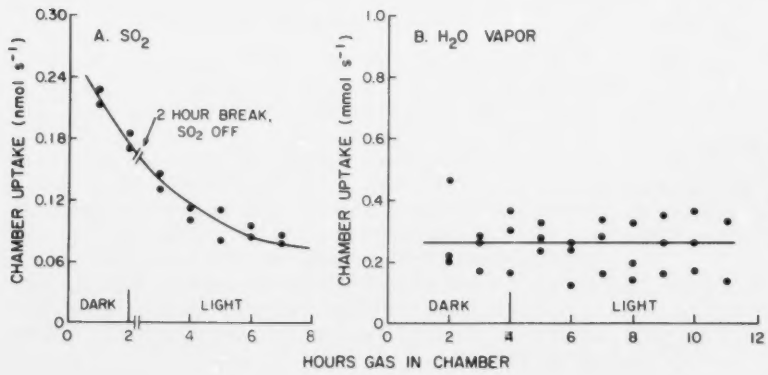

FIG. 1. Chamber uptake of SO_2 (A) and H_2O vapor (B) during SO_2 exposure. For SO_2, chamber uptake (nmol s^{-1}) = 0.0167 × (13.1891 − [4.3565 × ln h of SO_2 exposure]), where $r = 0.87$ and $n = 56$. For H_2O vapor, chamber uptake SE was 0.13 for $n = 116$. (●), Average of four observations.

Table 1. *Formulae Used on Gas Exchange Calculations (1, 11, 17, 23, 25)*

Component	Abbreviation	Units	Formulae and Assumptions
1. Chamber inlet concentration of gas	C_I	mol m^{-3}	
2. Chamber outlet concentration of gas	C_O	mol m^{-3}	
3. Change in gas concentration as it passes through chamber	C_x	mol m^{-3}	$C_x = C_I - C_O$
4. Air flow through chamber	F	m^3 s^{-1}	
5. Projected leaf area	A	m^2	Single-sided
6. Chamber uptake of gas	U	mol s^{-1}	$U = C_x \times F$
7. Conducting surfaces for leaf	CS		CS = (Adaxial + abaxial stomatal density) × (abaxial density)$^{-1}$
8. Total gas flux to leaves where Gas = SO_2 or H_2O vapor	J_{total}Gas	mol m^{-2} s^{-1}	J_{total}Gas = $\lvert([C_x \times F] - U)\rvert \times (2A)^{-1}$ where C_x is measured when plant is present, and $\lvert\ \rvert$ ensures that flux values for H_2O vapor are positive. The doubling of the area is required in order to consider SO_2 uptake by both adaxial and abaxial leaf surfaces.
9. Surface gas flux to leaves	$J_{surface}$Gas	mol m^{-2} s^{-1}	$J_{surface}$Gas = J_{total}Gas in dark for ABA treated plants
10. Internal gas flux to leaves	$J_{internal}$Gas	mol m^{-2} s^{-1}	$J_{internal}$Gas = $J_{total} - J_{surface}$
11. Correction factor for conductance from m s^{-1} to mol m^{-2} s^{-1}	CF		$CF = (P_{experimental}[\text{bar}] \times T_0\ [K^0]) \times (V_0\ [m^3\ mol^{-1}] \times P_0\ [\text{bar}] \times T_{experimental}[K^\circ])^{-1}$ where $T_0 = 2.73 \times 10^2$ °K, $V_0 = 0.0224$ m^3 mol^{-1}, and $P_0 = 1.01$ bar, all standard temperature and pressure conditions
12. Diffusion coefficient of SO_2 *versus* H_2O at boundary layer	D_a		$D_a = ([MW \text{ of } SO_2] \times [MW \text{ of } H_2O]^{-1})^{½}$ where MW of SO_2 = 64.06, MW of H_2O = 18.02
13. Diffusion coefficient of SO_2 *versus* H_2O at stomata	D_s		$D_s = ([MW \text{ of } SO_2] \times [MW \text{ of } H_2O]^{-1})^{-½}$
14. Boundary layer conductance of SO_2	g_aSO_2	mol m^{-2} s^{-1}	$g_aSO_2 = g_aH_2O \times D_a \times CF$ where g_aH_2O = 4.14 (boundary layer resistance to H_2O = 0.10 s cm^{-1} × CF)
15. Leaf conductance of H_2O vapor	g_lSO_2	mol m^{-2} s^{-1}	$g_lH_2O = (J_{internal}H_2O \times 2 \times CS) \times C_l^{-1} \times CF$, where C_l^{-1} (mol m^{-3}) is the change in concentration of H_2O vapor between leaf interior and ambient air based on leaf and air temperatures, respectively, *i.e.* vapor pressure deficit. The two adjusts the $J_{internal}H_2O$ back to a projected leaf area basis so that the conducting surface correction can be made.
16. Stomatal conductance of SO_2 based on H_2O vapor flux	g_sSO_2	mol m^{-2} s^{-1}	$g_sSO_2 = (g_lH_2O^{-1} - g_aH_2O^{-1}) \times D_s$
17. Cuticular concentration of SO_2	C_cSO_2	mol m^{-3}	$C_cSO_2 = C_o - (J_{surface}SO_2 \times g_aSO_2^{-1})$
18. Stomatal conductance of SO_2 based on SO_2 flux	g_mSO_2	mol m^{-2} s^{-1}	$g_mSO_2 = (J_{internal}SO_2 \times 2 \times CS) \times C_cSO_2^{-1} \times CF$, assumes concentration of SO_2 inside leaf is 0
19. Residual conductance of SO_2	g_rSO_2	mol m^{-2} s^{-1}	$g_rSO_2 = g_aSO_2 - g_sSO_2$
20. Epidermal conductance of SO_2	g_eSO_2	mol m^{-2} s^{-1}	$g_eSO_2 = J_{surface}SO_2 \times C_o^{-1} \times CF$

plants were at approximately the same stage of development as the plants used for the gas-exchange studies. Stomatal density was measured from leaf surface replicas obtained by applying clear fingernail polish to leaf surfaces. The replicas were removed from leaves, and stomatal counts made with a light microscope at 100 times power. Five fields of view were measured for one leaf from each of four plants. For *Pisum* the adaxial and abaxial counts were from opposite sides of the midvein from the same leaflet; different leaves were used for counts from the other three species. Stomatal density was measured in midmorning on sunny days, approximately 4 to 6 h after sunrise.

The stomatal density values were used to determine leaf conducting surface correction factors according to formulae adapted from Korner *et al.* (17) and given in formula 7 on Table I. The projected leaf area values were then multiplied by the conducting surface correction factors to obtain a corrected leaf area. This corrected area formed the basis for the internal SO_2 and H_2O vapor flux values used to calculate components of leaf conductance to SO_2.

Four plants of each species were used to determine SO_2 and H_2O flux for these studies, thus providing four single plant replicates per measurement. Analysis of variance, one-tailed *t* tests, and regression analyses were used for statistical analyses (22). All significant differences were determined at the $p < 0.05$ level.

RESULTS

Flux of SO_2 and H_2O. Total flux of SO_2 to both adaxial and abaxial leaf surfaces was quite variable across all four species, ranging from 2.7 to 16.8 nmol m^{-2} s^{-1} in the dark, and 8.3 to 25.4 nmol m^{-2} s^{-1} in the light (Fig. 2A). The dark $J_{total}SO_2$ was lowest in *Pisum*, 2 and 3 times higher in *Geranium* and *Diplacus*, respectively, and over 6 times higher in *Lycopersicon*. In the light $J_{total}SO_2$ was similar for *Pisum*, *Geranium*, and *Diplacus*, but over twice as high in *Lycopersicon* compared to the other species.

In the dark, SO_2 flux values for ABA-treated *Pisum*, *Lycopersicon*, and *Diplacus* plants (dashed lines, Fig. 2A), were 31, 44, and 32%, respectively, lower than for plants without ABA (dark bars). The lower fluxes were attributed to further stomatal closure induced by ABA. Thus, the dark plus ABA values were the best representation of SO_2 flux solely to leaf surfaces. In *Geranium*, the ABA treatment resulted in SO_2 flux values of 6.6 ± 1.3 nmol m^{-2} s^{-1}, or approximately the same as for dark without ABA plants (5.3 ± 1.3 nmol m^{-2} s^{-1}). Thus, the values in the dark without ABA were used to represent surface uptake of SO_2 of *Geranium* only. For all species surface flux was assumed to be the same in light and darkness.

Total flux of H_2O vapor also was variable, ranging from 0.4 to 1.9 mmol m^{-2} s^{-1} in the dark, and from 1.2 to 2.2 mmol m^{-2} s^{-1} in the light (Fig. 2B). In the dark $J_{total}H_2O$ was lowest in *Geranium* and highest in *Lycopersicon*. In the light $J_{total}H_2O$ was similar for *Pisum*, *Geranium*, and *Diplacus* but was twice as high in *Lycopersicon*.

Water vapor flux from ABA-treated plants ranged from 0.3 to 1.3 mmol m^{-2} s^{-1} in the dark for *Pisum*, *Lycopersicon*, and *Diplacus* (Fig. 2B). These dark plus ABA values were lower than the dark alone values, and thus were used to estimate actual surface flux (cuticular transpiration) of H_2O vapor from leaves. In *Geranium* the dark alone values were used for surface H_2O vapor flux for the same reasons given for surface SO_2 flux.

An evaluation of SO_2 absorbed through stomata ($J_{internal}SO_2$) was made on a both-leaf-surfaces basis by subtracting $J_{surface}SO_2$ from $J_{total}SO_2$. Internal flux to *Pisum*, *Lycopersicon*, *Geranium*, and *Diplacus* plants, respectively, was 0.9 ± 0.5 SE, 8.5 ± 3.6, 0, and 2.7 ± 1.1 nmol m^{-2} s^{-1} in the dark; and 6.5 ± 0.7, 16.7 ± 2.8, 5.2 ± 1.2, and 3.8 ± 1.0 nmol m^{-2} s^{-1} in the light. On the same both-leaf-surfaces basis, $J_{internal}H_2O$ through stomata from

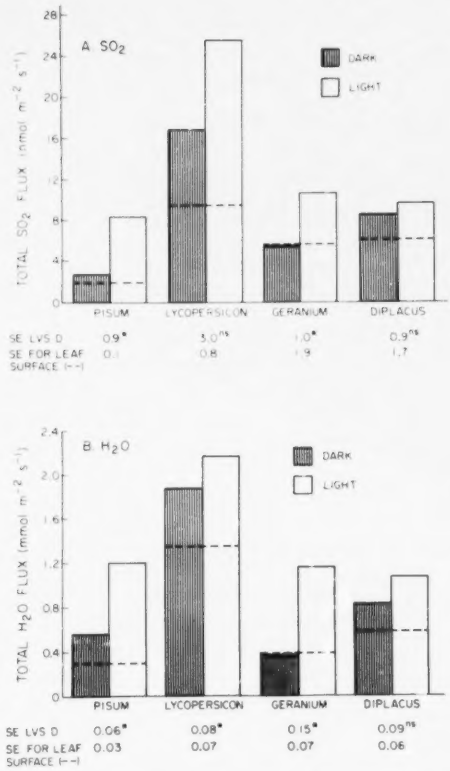

FIG. 2. Interspecific variation in flux of SO_2 (A) and H_2O vapor (B) to plants. Full bars, total flux in the dark and light; dashed lines, surface flux measurements (dark + ABA). The segment of the bars above the dashed lines indicates internal flux of SO_2 entering leaves (A), or H_2O vapor flux exiting leaves (B). Values are averages of four observations. Flux is on a 'both-leaf-surfaces' basis for all species. For $J_{total}SO_2$ light *versus* dark differences for *Pisum* and *Geranium* are significantly different at $p < 0.05$. For $J_{total}H_2O$ light *versus* dark difference for *Pisum*, *Lycopersicon*, and *Geranium* are significantly different at $p < 0.05$. Standard errors for $J_{surface}SO_2$ and $J_{surface}H_2O$, and for comparing light *versus* dark $J_{total}SO_2$ or $J_{total}H_2O$ valus are indicates below species names.

Table II. *Stomatal Density for Four Plant Species*

Values are averages ± SE for 20 observations for stomatal density (five fields of view from each of four plants). Conducting surfaces = (adaxial stomatal density + abaxial density)/abaxial stomatal density.

Species	Surface	Stomatal Density	Relative Conducting Surfaces
		no. mm^{-2}	
Pisum	Adaxial	16 ± 9	1.500
	Abaxial	32 ± 12	
Lycopersicon	Adaxial	53 ± 3	1.525
	Abaxial	99 ± 5	
Geranium	Adaxial	11 ± 1	1.107
	Abaxial	103 ± 3	
Diplacus	Adaxial	0	1.000
	Abaxial	85 ± 7	

Table III. *Components of Leaf Conductance of SO_2 for Four Plant Species*

Values are averages ± SE for four observations, calculated according to formulae as shown given in Table I, using the conducting surfaces shown in Table II. The g_sSO_2 values are based on subtraction of g_sSO_2 from g_mSO_2 for individual plants. The g_mSO_2 was estimated as 2.71 mol m^{-2} s^{-1} for all four species.

Species	g_sSO_2	g_mSO_2	g_rSO_2	g_cSO_2
		mol m^{-2} s^{-1}		
Pisum	0.105 ± 0.003	0.081 ± 0.009	−0.024 ± 0.009	0.017 ± 0.005
Lycopersicon	0.132 ± 0.011	0.192 ± 0.015	0.059 ± 0.025	0.088 ± 0.003
Geranium	0.122 ± 0.025	0.087 ± 0.017	−0.036 ± 0.019	0.050 ± 0.010
Diplacus	0.070 ± 0.013	0.071 ± 0.019	0.002 ± 0.016	0.053 ± 0.001

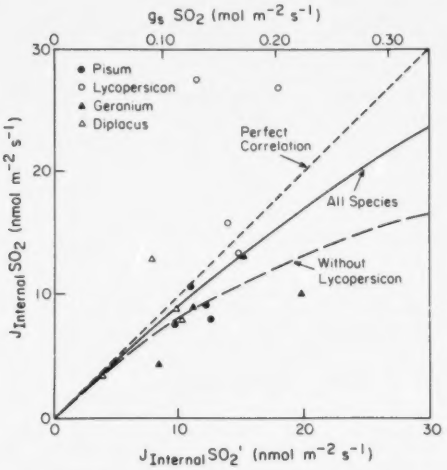

FIG. 3. Internal SO_2 flux based on water vapor diffusion ($J_{internal}SO_2'$) *versus* internal SO_2 flux based on direct measurement of SO_2 uptake ($J_{internal}SO_2$). $J_{internal}SO_2 = J_{internal}SO_2' \times ([J_{internal}SO_2' \times 0.0045] + 1.1118)^{-1}$, $r = 0.72$, and $n = 16$ for all species (——). $J_{internal}SO_2 = J_{internal}SO_2 \times ([J_{internal}SO_2' \times 0.0273] + 1.0039)^{-1}$, $r = 0.74$, and $n = 12$ for three species without *Lycopersicon* (— —). Values for $J_{internal}SO_2'$ are calculated as $g_sSO_2 \times$ % SO_2 in the chamber (1.1×10^{-7}%), values for $J_{internal}SO_2$ were calculated as described in Table I. The scale above the figure indicates g_sSO_2 values for the data points. (– – –), A perfect theoretical linear relationship between $J_{internal}SO_2$ and $J_{internal}SO_2'$.

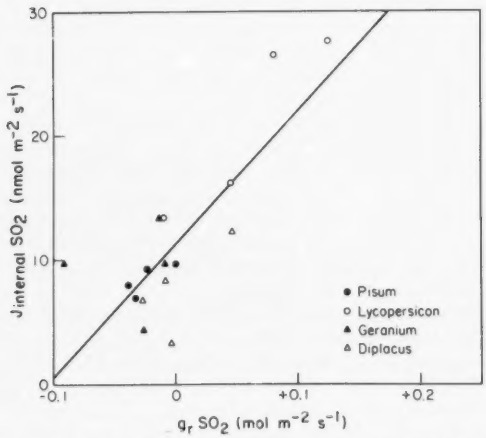

FIG. 4. Residual conductance of SO_2 *versus* internal SO_2 flux for all plants $J_{internal}SO_2 = (g_sSO_2 \times 107.62) + 11.47$, $r = 0.79$ and $n = 16$.

Pisum, *Lycopersicon*, *Geranium*, and *Diplacus*, respectively, was 0.23 ± 0.05, 0.55 ± 0.05, 0, and 0.17 ± 0.09 nmol m^{-2} s^{-1} in the dark; and 0.88 ± 0.02, 0.83 ± 0.09, 0.79 ± 0.17, and 0.42 ± 0.08 nmol m^{-2} s^{-1} in the light. *Geranium* had essentially no $J_{internal}SO_2$ or $J_{internal}H_2O$ in the dark, and *Lycopersicon* had the highest $J_{internal}SO_2$ and $J_{internal}H_2O$ in the dark. *Diplacus* had the lowest $J_{internal}SO_2$ and $J_{internal}H_2O$ in the light. *Lycopersicon* had the highest $J_{internal}SO_2$ in the light, and *Pisum*, *Lycopersicon*, and *Geranium* all had similar $J_{internal}H_2O$ values in the light.

For *Pisum* and *Lycopersicon* the $J_{surface}SO_2$ was approximately 35% of $J_{internal}SO_2$ (both on a both-leaf-surface basis), as described for other cultivated species. *Geranium* had a surface SO_2 flux of 5.3 nmol m^{-2} s^{-1} that was 50% of $J_{internal}SO_2$. This was proportionally more than the 9.7 nmol m^{-2} s^{-1} or 33% of $J_{internal}SO_2$ reported for *Geranium* plants exposed to 12.44 μmol m^{-3} SO_2 (0.03 μl/l) (24, modified for both-leaf-surfaces). *Diplacus* had a $J_{surface}SO_2$ of 5.7 nmol m^{-2} s^{-1}, or 140% of $J_{internal}SO_2$. the high $J_{surface}SO_2$ was expected as *Diplacus* has glandular leaf surfaces, a characteristic that provides highly absorptive areas for SO_2 uptake (3). Winner and Mooney (28) also reported a $J_{surface}SO_2$ of approximately 6.0 nmol m^{-2} s^{-1} for *Diplacus*. However, in their study this was only 67% of $J_{internal}SO_2$ for plants exposed to 10.36 μmol m^{-3} (0.25 μl/l) SO_2.

Leaf Conductance Components. Comparison of SO_2 conductances for the four species required careful consideration of the proper leaf area basis for $J_{internal}H_2O$ and $J_{internal}SO_2$ values used in the calculations, based on the relative stomatal densities on adaxial and abaxial leaf surfaces. Stomatal densities for adaxial leaf surfaces were 53.5, 50, and 10.7% of the densities on the abaxial surfaces for *Lycopersicon*, *Pisum*, and *Geranium*, respectively (Table II). There were no stomata on the adaxial surfaces of *Diplacus* leaves. Therefore, relative conducting surfaces used in determining the leaf area basis for $J_{internal}SO_2$ and $J_{internal}H_2O$ for conductance calculations ranged from 1.525 in *Lycopersicon* to 1.0 in *Diplacus*.

Conductance of SO_2 based on H_2O vapor loss through stomata(g_sSO_2), ranged from 0.07 to 0.13 mol m^{-2} s^{-1} (Table III). Conductance of SO_2 based on internal SO_2 flux (g_mSO_2) was sightly lower than g_sSO_2 for *Pisum* and *Geranium*, essentially the same as g_sSO_2 for *Diplacus*, and much higher than g_sSO_2 for *Lycopersicon*. Based on the individual plant data from all species, internal SO_2 flux calculated from the g_sSO_2 data ($J_{internal}SO_2'$) was correlated with the $J_{internal}SO_2$ values based on direct SO_2 uptake measurements (Fig. 3). However, the data fit an asymptotic curve ($r = 0.72$) and not a straight line ($r = 0.26$), indicating that other factors in addition to the stomata may limit SO_2 uptake especially at higher SO_2 uptake rates. Without *Lycopersicon*, the data for the other three species also fit an asymptotic curve, but one where the $J_{internal}SO_2'$ diverged from $J_{internal}SO_2$ even more as the $J_{internal}SO_2$ increased.

The differences between g_mSO_2 and g_sSO_2 (*i.e.* g_rSO_2 or residual conductance), ranged from −0.04 to +0.06 mol m^{-2} s^{-1} (Table III). These values indicated that the actual conductance of SO_2 into leaves ranged from less than (negative g_rSO_2) to greater than

Table IV. *Variation in Pisum sativaum Leaf Conductance Components with Differing Assumptions for Gas Exchange Calculations*

Values are averages of four observation ± SE for *Pisum sativum* and were calculated according to formulae given in Table I. The $J_{internal}H_2O$ flux represents flux through the stomata from the inside of leaves. The number of conducting surfaces indicated are used to calculate all parameters.

Method for J Surface	H_2O Flux Used	Relative No. Conducting Surfaces	$J_{internal}SO_2$	g_sSO_2	g_mSO_2	g_rSO_2
			nmol m^{-2} s^{-1}		*mol m^{-2} s^{-1}*	
ABA + dark	$J_{internal}$	2.0	6.5 ± 0.7	0.078 ± 0.002	0.060 ± 0.007	−0.017 ± 0.007
		1.5	8.8 ± 0.8	0.105 ± 0.003	0.081 ± 0.009	−0.024 ± 0.009
		1.0	13.0 ± 1.4	0.161 ± 0.004	0.121 ± 0.012	−0.039 ± 0.013
	J_{total}	2.0	6.5 ± 0.7	0.108 ± 0.003	0.060 ± 0.007	−0.047 ± 0.007
		1.5	8.8 ± 0.8	0.145 ± 0.004	0.081 ± 0.009	−0.065 ± 0.009
		1.0	13.0 ± 1.4	0.226 ± 0.006	0.121 ± 0.014	−0.107 ± 0.015
Dark	$J_{internal}$	2.0	5.6 ± 0.6	0.057 ± 0.006	0.053 ± 0.007	−0.004 ± 0.007
		1.5	7.5 ± 1.6	0.077 ± 0.008	0.071 ± 0.009	−0.006 ± 0.009
		1.0	11.2 ± 1.2	0.117 ± 0.011	0.107 ± 0.014	−0.011 ± 0.028
	J_{total}	2.0	5.6 ± 0.6	0.108 ± 0.003	0.053 ± 0.007	−0.055 ± 0.009
		1.5	7.5 ± 1.6	0.145 ± 0.004	0.071 ± 0.009	−0.075 ± 0.011
		1.0	11.2 ± 1.2	0.226 ± 0.006	0.107 ± 0.014	−0.119 ± 0.018
H_2O surrogate	J_{total}	2.0	11.2 ± 0.6	0.108 ± 0.003	0.108 ± 0.003	0
		1.5	15.6 ± 0.8	0.145 ± 0.004	0.145 ± 0.004	0
		1.0	21.8 ± 1.2	0.226 ± 0.006	0.226 ± 0.006	0
	$J_{internal}$	1.5	11.3 ± 0.9	0.077 ± 0.008	0.077 ± 0.008	0

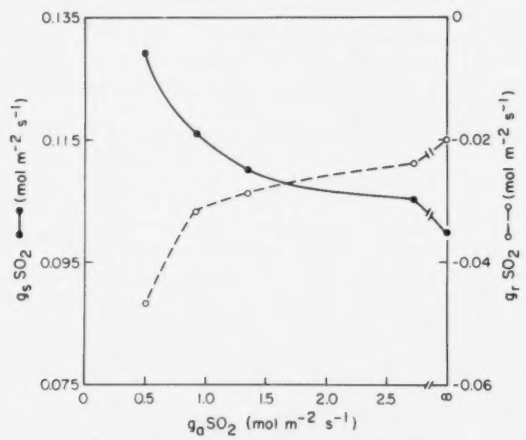

FIG. 5. Estimated stomatal and residual conductance of SO_2 *versus* different sample values for boundary layer conductance of SO_2.

(positive g_rSO_2), the rates derived solely from g_sSO_2 values. For *Pisum*, *Geranium*, and *Diplacus* g_rSO_2 values were generally less than or equal to zero (Fig. 4). In *Lycopersicon* the g_rSO_2 difference was considerably greater than zero for three plants and just less than zero for one plant. The relationship between g_rSO_2 and $J_{internal}SO_2$ best fit a linear equation ($r = 0.79$), with more positive g_rSO_2 values correlated with higher $J_{internal}SO_2$ values.

Epidermal conductance of SO_2 (g_cSO_2) ranged from 0.02 to 0.09 mol m^{-2} s^{-1} (Table III). Thus, g_cSO_2 was from 16% (*Pisum*) to 76% (*Diplacus*) of g_sSO_2 in the light.

Sensitivity Analysis of Flux and Conductance in Pisum. Values of SO_2 flux and conductance varied considerably depending on the assumptions used in their calculation. Use of only dark values for determining surface flux resulted in 14% lower $J_{internal}SO_2$ estimates than when using dark plus ABA conditions (Table IV). Use of only dark surface values resulted in approximately unchanged to 25% lower g_sSO_2, 13% lower to 33% higher g_mSO_2, and 50% lower to 50% higher g_rSO_2 than dark plus ABA values. However, g_rSO_2 remained negative for this data set, and never became zero or positive irrespective of the assumptions made in its calculation.

Previous studies had used total H_2O vapor flux (H_2O surrogate method) as the basis for calculating g_sSO_2 (27). Use of the flux of H_2O vapor out through stomata ($J_{internal}$) resulted in lower g_sSO_2 and g_rSO_2 values than when total H_2O vapor flux (J_{total}) was used (Table IV).

Calculations using one relative conducting surface compared to 2.0 conducting surfaces resulted in greater internal SO_2 flux values in inverse proportion to the decrease in area (Table IV). Values of g_sSO_2 increased in inverse proportion to surface area, doubling as the surface area was halved. Values of g_mSO_2 increased as surface area decreased; however, the increase was by 300 to 400% with a halving of area. The g_rSO_2 values generally became more negative as surface area decreased.

The H_2O surrogate method resulted in $J_{internal}SO_2$ values of from 11.2 to 21.8 μmol m^{-2} s^{-1} depending on the surface area used in the equations (Table IV). These estimates of $J_{internal}SO_2$ are greater than the $J_{total}SO_2$ values actually measured in the study; *e.g.* 8.3 and 16.6 nmol m^{-2} s^{-1} assuming two and one conducting surface areas, respectively. With the H_2O surrogate method all g_sSO_2 values were the same as for other methods and g_mSO_2 was assumed to be the same as g_sSO_2 (Table IV). All g_rSO_2 values were assumed to be zero.

Variation in g_aSO_2 in calculations had little effect on g_sSO_2 over the normal range of g_aSO_2 values found in plants (Fig. 5) (assuming the same total leaf conductance of SO_2 and H_2O). Between g_aSO_2 values of 0.93 and 2.71 mol m^{-2} s^{-1} (boundary layer resistances of 0.3 and 0.1 s cm^{-1}, respectively), g_sSO_2 decreased by only 10%. As g_aSO_2 decreased below 0.93 mol m^{-2} s^{-1} g_sSO_2 increased greatly. The lowest g_sSO_2 occurred when g_aSO_2 was assumed to be infinite (boundary layer resistance of

zero). Decreased g_mSO_2 resulted in decreased g_sSO_2 values. Between g_mSO_2 of 0.93 and 2.71 mol m^{-2} s^{-1} g_sSO_2 decreased by 33%. Values of g_sSO_2 decreased rapidly as g_mSO_2 decreased below 0.93 mol m^{-2} s^{-1}.

DISCUSSION

Interspecific Variability in SO_2 Flux. These studies further documented both the similarities and differences in SO_2 flux among plant species exposed to the same ambient SO_2 concentration. Three species representing divergent types of plants: *Pisum* (crop), *Geranium* (native herbaceous plant—eastern United States), and *Diplacus* (native woody plant—mediterranean climate in California), had similar total SO_2 flux values. However, the mutant *Lycopersicon* plants had over twice the total SO_2 flux of the other species.

Conductance and SO_2 Flux. The high correlation between $J_{internal}SO_2$ and g_sSO_2 for all species in these studies supported the suggestion that stomatal conductance is the major determinant of internal SO_2 uptake (27). Data from the mutant *Lycopersicon* clouded the picture somewhat, for at a g_sSO_2 of 0.1 to 0.2 mol m^{-2} s^{-1} it had a $J_{internal}SO_2$ two to three times the other species.

The clustering of most g_sSO_2 values at zero or just below zero indicated that the $J_{internal}SO_2$ was very close to values expected from g_sSO_2 for many plants. The lowest g_sSO_2 values occurred at low $J_{internal}SO_2$ values typical with ambient concentrations of SO_2. The lack of an apparent internal conductance for *Diplacus* followed the hypothesis of Winner and Mooney (27). Thus, leaf internal factors in general had comparatively little effect on SO_2 movement from the stomata into the gas-liquid interface at the cellular surfaces as g_sSO_2 values were much less than g_sSO_2 values for all species except *Lycopersicon*. The negative residual conductance values for some plants suggested that physical or chemical factors inside leaves can obstruct the free diffusion of SO_2 into cells (12), but only to a slight extent compared to inhibition of diffusion by stomata.

The greater g_sSO_2 than g_mSO_2 for *Pisum* resulted in the greater $J_{internal}SO_2'$ than $J_{internal}SO_2$ rates (Fig. 4). This difference may represent an overestimation of SO_2 absorption by the H_2O surrogate *versus* the mass balance procedure, due to inhibition of SO_2 diffusion within leaves. The difference also may result from an underestimation of SO_2 absorption by the mass balance compared to the H_2O surrogate procedure possibly due to overestimation of surface uptake in the light. A smaller stomatal SO_2 diffusion coefficient (D_s) of 0.50 could have been used as suggested by Winner *et al.* (29), compared to the 0.53 used in this study. However, this substitution would have decreased $J_{internal}SO_2'$ by only 6%, bringing it only a little closer to $J_{internal}SO_2$.

Geranium did not exhibit positive residual conductance values (negative residual resistance) as reported previously (25). However, the earlier studies used SO_2 concentrations at or above 12.44 μmol m^{-3} (0.3 μl/l). The resulting SO_2 concentration gradient from the ambient air to the assumed zero concentration within leaves in the previous research was greater than the 4.56 μmol m^{-3} to zero gradient reported here. This greater SO_2 gradient may have triggered processes for rapid metabolism of SO_2. These processes, such as the photoreduction of SO_2 and consequent reemission of sulfur as H_2S, may take place only after a threshold level of SO_2 uptake is exceeded (25). The resulting rapid turnover of SO_2 could be coupled with active uptake processes providing for greater SO_2 flux into cells than can be accounted for by simple diffusion (25).

The factors in *Lycopersicon* responsible for the large uptake of SO_2 were not investigated, but were responsible for the larger g_mSO_2 than g_sSO_2 which resulted in the positive g_sSO_2 values. For *Lycopersicon* the permanently open stomata, or changes in leaf structure or metabolism associated with the ABA deficiency may be responsible for the large SO_2 uptake. For example, the rate of stomatal conductance by itself can affect residual or mesophyll conductance (21). It also is possible that 0.1 mM ABA was not adequate for maximal stomatal closure, and thus surface flux of SO_2 was overestimated and internal flux of SO_2 underestimated. However, flux of H_2O from leaf surfaces would also have been overestimated resulting in an essentially unchanged proportional relationship between $J_{internal}SO_2$ and $J_{internal}H_2O$, and thus between g_mSO_2 and g_sSO_2.

Assumptions Used in Gas Exchange Calculations. Values for SO_2 flux and conductance cannot be measured directly, but are the product of basic SO_2 concentration, and H_2O vapor pressure deficit (dew point and leaf temperature measurements). To produce meaningful SO_2 gas exchange values, various assumptions must be applied to these formulae, resulting in variable data depending on considerations such as method for determining surface *versus* stomatal flux for SO_2 and H_2O vapor, and how the leaf surface area is calculated. Based on the particular assumptions used, gas exchange values can vary by 2 to 3 times in the same species. However, the sign on conductance components such as g_sSO_2 should not change (Table IV).

The ABA method has promise for accurate measurement of surface flux, especially if the optimum ABA concentration for maximum stomatal closure is determined. For species in which stomata do not close completely in the dark (7), ABA treatment may be the only possible procedure for determining surface flux. A concentration of 0.1 mM ABA was used in these studies; other concentrations should be tested for maximum closure in other species. However, the possibility remains that surface flux may actually change in the light *versus* dark, as cuticular uptake of materials is known to change with time during the photoperiod (8).

A potential problem for all data obtained with whole leaf chambers is the derivation of stomatal conductance representing a flat single leaf surface, but based on flux measurements from two surfaces. If species with different adaxial:abaxial stomatal densities are to be compared based on whole leaf measurements, then a 'conducting surface' correction of some sort may account for the fact that the actual SO_2 or H_2O vapor flux is through different relative leaf areas. The conducting surface procedure based on 'stomata covered leaf area' described by Korner *et al.* (17) may be appropriate. Stomatal density values may not precisely indicate the true relative flux of gas to or from adaxial *versus* abaxial leaf surfaces due to differences in the extent of stomatal closure between the two surfaces (19). However, it is not possible to factor this dynamic stomatal response into conductance calculations based on whole plant chamber measurements.

In conclusion, stomatal conductance is the major factor in determining internal plant flux of SO_2. Internal factors can decrease the flux into leaves, but the flux inhibition is much less than that due to stomata. This was shown by the lower calculated SO_2 flux based on water vapor loss compared to actual SO_2 uptake measurements for *Pisum* and *Geranium*. The internal factors also can increase the flux of SO_2 into leaves as shown by the large flux of SO_2 to the *Lycopersicon* mutant, a plant with unusual gas exchange characteristics. The divergent results previously reported for SO_2 flux and conductance may in large part be due to species used, SO_2 concentration, and differences in the assumptions used to model SO_2 uptake by plants. A simple model for SO_2 uptake into leaves can take into account all previous results: gaseous uptake of SO_2 through stomata (primary control point), followed by transfer into cells which can prove to either inhibit or enhance uptake under certain conditions (secondary control point) (26). This model indicates that while stomatal conductance can provide a general estimate of SO_2 absorption into leaves, actual measurements of SO_2 uptake would

more precisely describe the biochemically active dose of SO_2 inside leaves.

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